Fisheries-induced changes of shoaling behaviour: Mechanisms and potential consequences

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Abstract

We outline key mechanisms by which fishing can change the shoaling tendency and collective behaviour of exploited species - an issue that is rarely considered and poorly understood. We highlight potential consequences for fish populations and food webs, and discuss possible repercussions for fisheries and conservation strategies.

Keywords: collective behaviour, fisheries-induced evolution, food web, harvesting, predator-prey interactions, shoaling, schooling

Shoaling behaviour and fisheries

Capture fisheries can exert strong pressures on exploited fish species, altering life histories, size and age structure, and population density. Intensive fishing can also affect fish behaviour by selectively removing individual phenotypes that are more vulnerable to specific fishing techniques [1, 2]. What has so far largely escaped attention is that fishing may also affect the shoaling tendency and collective behaviour of fish [1-5]. Shoaling can be defined as fish that socially group together, from simply aggregating and interacting in time and space to directed and coordinating movements, such as schooling. Grouping has strong adaptive value for many fish species, influencing predation risk, resource acquisition, and the spread of information [5]. Therefore, if fisheries would induce changes to shoaling it could have relevant ecological consequences for exploited species [4]. Previous reviews have indeed suggested that fishing could change shoaling behaviour by altering individual behavioural phenotypes, especially boldness [1, 2]. We go beyond these studies and propose parallel pathways by which fishing can affect collective behaviour at individual, group, and population levels (Fig. 1). We end by outlining potential ecological consequences and repercussions for fisheries and biodiversity conservation strategies.

Mechanisms by which fishing can alter shoaling behaviour

Fishing can directly affect shoaling behaviour by targeting individual phenotypes [1, 2]. Changes in the phenotypic composition and heterogeneity of exploited species can in turn shape the emergent properties of fish shoals, such as shoal size, cohesion, and among-group dynamics, via individual-level changes in behaviour and social interactions [7]. We outline four possible pathways that could be acting in parallel.

First, as previously identified [1, 2], fishing may affect shoaling by directly selecting on individual behaviour and physiological traits [4, 6-8]. For example, there is accumulating evidence that a number of fishing techniques, including hook-and-line, trapping, gillnetting, and spearfishing, selectively harvest bold, aggressive and more active phenotypes [1]. As these phenotypes are often linked to leadership, their selective removal, and the resulting homogenization of phenotypic traits, may have disruptive effects on the coordination and movement tendencies of fish shoals [6]. Some techniques, such as hook-and-line fishing, may also selectively target social phenotypes [7], which can result in a decrease in shoaling tendency and fish to form smaller groups [4]. Even shy fish may be selectively targeted by some fishing techniques, such as by trawling, as shyer fish are more likely to shoal than explore by themselves, which could also result in an overall reduction in sociability of exploited species [2]. Fisheries-induced changes of shoaling behaviour can also arise through selection operating on physiological phenotypes that correlate with behaviour. For example, trawling may selectively target individuals with reduced anaerobic capacity and burst swimming performance [8], thereby decreasing heterogeneity of these traits and potentially resulting in faster moving shoals with higher endurance [6]. Many exploited fish species, such as small pelagics, tend to occur in very large shoals. In these situations, despite individuals strongly conforming in their behaviour, as a result of trait-selective harvesting small differences between individuals can still accumulate over time and result in spatial differences within shoals as well as changes in group behaviour and among-shoal assortment [6].

Second, the intense and positive size-selective mortality imposed by many fisheries results in demographic changes and may lead to evolution of fast life-histories [9]. Fast life histories are correlated with certain behavioural and physiological traits, such as increased risk-taking behaviour and a smaller aerobic scope. Harvesting-induced changes toward fast life-histories can thus also indirectly change shoaling behaviour [1, 2, 6, 8]. Indeed, changes in behaviour are possible even in completely unselective fisheries where life-histories adapt to elevated fishing mortality levels [10]. Additional mechanisms could be at play that relate to morphological and demographic factors, specifically in relation to fisheries-induced demographic downsizing of individuals. In many species, body size is closely linked to optimal and maximum movement speed, which has been shown to influence collective behaviour. Specifically, shoals of smaller individuals could be more cohesive, slower in movement and less coordinated [6]. Selective removal of large individuals could also reduce shoal cohesion because the surviving smaller and possibly shyer fish may show an increased attention to environmental over social cues [3].

Third, fishing may directly affect shoal size by targeting large fractions or even entire shoals. Larger shoals are more easily detected, such as through echo sounding used in purse seining fisheries (Box 1). Thus, when detected, fish in larger shoals are more at risk to be captured. Fish of certain species may also be more likely to enter into fishing traps when in larger shoals [11]. Over time such effects can result in a strong reduction of shoal sizes of exploited populations, both as a consequence of fishing mortality as well as by fishing effects on behaviour and the composition of phenotypes in the population, as explained above.

Fourth, by intensive fishing, the population size and thereby local density of exploited species tends to be considerably reduced, possibly inducing a series of density-dependent effects on shoal size and cohesion [5]. For example, at low population densities, a reduced encounter rate between individuals is likely to result in a reduction in shoal sizes. Importantly, as the population density of predators and prey tends to be strongly linked, fisheries-induced changes in population density of one trophic level is likely to have repercussions on the density and shoaling behaviour of another trophic level through species interaction effects. A higher predator density is for example expected to increase the shoaling tendency of prey to mitigate the increased risk of predation. Such behavioural responses may be shaped by, or even be reversed due to fisheries-induced changes of shoaling behaviour, which would often involve a decrease, rather than an increase, in shoaling (Box 1).

Potential ecological consequences and repercussions for fisheries and conservation

Relative to the strong effects of biomass extraction or age and size-truncation in response to intensive harvesting, fisheries-induced changes of shoaling may only seem of secondary relevance. However, obligate schooling (e.g., small pelagic fish) and shoaling species (e.g., tunas) have important ecological roles in aquatic food webs and sustain a great part of global fisheries. Hence, the mechanisms described may have notable consequences for ecosystem functioning, and repercussions for fisheries and biodiversity conservation strategies.

From an ecological perspective, fisheries-induced changes of shoaling behaviour could elevate natural mortality and thus affect population dynamics [3]. A reduction in shoaling could also weaken predator-prey interactions due to a reduced vulnerability of prey to predators [1]. Such effects could be aggrevated by additionally targeting shoaling predators (e.g., tunas), because of a possible reduction in their foraging efficiency, thereby modifying trophic flow. Yet, under intense harvesting of larger individuals, fisheries-induced decrease of shoal cohesion could also strengthen predator-prey interactions because prey could become more vulnerable to natural predators [3]. A fisheries-induced reduction of shoal size is more likely for obligate (e.g., small pelagics) than for facultative schooling species, rendering the former considerably harder to find and catch, including by natural predators [4]. Thus, changes of shoaling behaviour and shoal size in response to fishing can affect population dynamics and trophic flow and thereby affect predator-prey interactions and ecosystem functioning.

From a socio-economic perspective, specifically a fisheries perspective, a reduction in shoaling could impact catch rates and fish detectability, which will negatively impact the operating costs and yield of commercial fisheries and could reduce the benefits generated by recreational fisheries, as it is dependent on sufficient catch rates, with repercussions for the local economy. [1]. Moreover, mechanisms that maintain group size at declining population density [4, 5] may foster hyperstable catch rates - i.e. catch rates remaining high even at low abundances - thereby increasing the probability of unexpected stock collapses [5]. Importantly, changes in shoaling behaviour may slowly decouple catch rates and stock abundance, which can negatively affect the ability of researchers and managers to assess fish stock status and thus potentially inform wrong management practices and policies. Multispecies and ecosystem models deployed to project fish biomass and inform management actions may suffer from these limitations too.

Limitations and future research

Most of the arguments we present are theoretical, or based on empirical evidence generated from small-bodied freshwater fish. The prevalence of the mechanisms and consequences in exploited fish populations are therefore not yet fully known. We specifically lack knowledge for which exploited species and what fishing techniques we can expect the largest impacts on shoaling. A key next step is to collect long-term data of shoaling behaviour of exploited species in the wild from areas differing in fishing pressure, and use experimental and modelling approaches to examine the impacts of different fishing techniques and harvest policies. It would also be valuable to better integrate the local knowledge of fishers into data collection and the interpretation of results (Box 1). Novel empirical findings should be used to inform and calibrate assessment and social-ecological models aimed at understanding and quantifying impacts of fisheries on shoaling across different levels of biological organization, with the ultimate goal to contribute to the sustainable management of fish populations.

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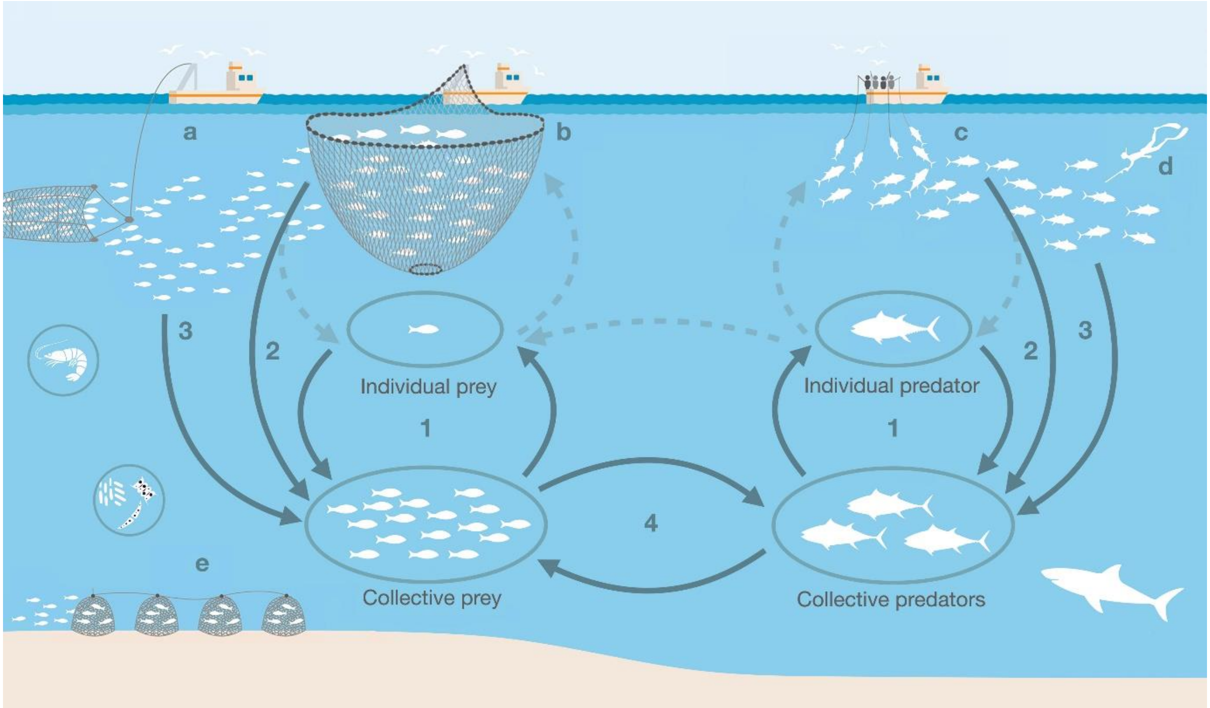

Figure 1. Parallel pathways affecting fisheries-induced changes of shoaling behaviour. Changes of shoaling can occur through plastic (e.g. gear avoidance learning), demographic (e.g. changes in age/size composition and density), and evolutionary processes (e.g. changes of heritable traits). Intensive fishing may change the phenotypic composition of exploited populations, in particular related to life-history, behavioural, and physiological traits, such as growth rate, sociability, boldness, swimming capacity and metabolic rate. These changes can in turn directly impact the shoaling behaviour of both prey and predators (1). Fishing can also directly (2), by targeting larger shoals, or indirectly (3), by influencing population density, change fish group dynamics. The direction of such fisheries-induced changes depends on the fishing gear and technique used (a-e). Predictions may be most feasible for species that are exploited almost exclusively by one fishing gear (e.g. purse seiners in small pelagics fisheries; Box 1), but the difficulty in monitoring behaviour in natural settings complicates the testing of predictions in situ. Yet, the majority of fish species is simultaneously exploited by multiple fishing techniques, whose cumulative effects on shoaling behaviour are still poorly understood. Fisheries-induced changes of shoaling can affect energy flows within food webs through bottom-up and/or top-down mechanisms that can alter the functional responses (4). Dashed arrows represent alternative pathways linking shoaling behaviour to fisheries (e.g. reduction of catchability). Drawings of fishing techniques copyrighted and courtesy of the Marine Stewardship Council / Steve Rocliffe.

Box 1. A case study of small pelagics fisheries

In the North-Western Mediterranean, small pelagics such as sardines (*Sardina pilchardus*) and anchovies (*Engraulis encrasicolus*) support purse seine fisheries, Figure I. Over the last decades, biomass and landings of small pelagics in the area have substantially dropped and catches have been increasingly of smaller-sized fish [12]. Anecdotal evidence by fishers suggests that the drop in captures of small pelagics may be related to changes in their behaviour. In particular, fishers are reporting that small pelagics do no longer form as large and cohesive groups as in the past, and are generally less accessible to fishing. Fishers associate these behaviours to the increasing presence of bluefin tuna (*Thunnus thynnus*), whose abundance locally increased after the establishment of effective tuna management measures [12]. In general, risk of predation is expected to trigger increased cohesion rather than prey splitting in smaller and more dispersed shoals [5]. However, the various mechanisms we explain here could underlie the observed changes in shoaling behaviour, link to changes in the phenotypic composition of shoals caused by fisheries. and thereby explain why small pelagics no longer show the expected shoaling behaviour in the presence of tunas.

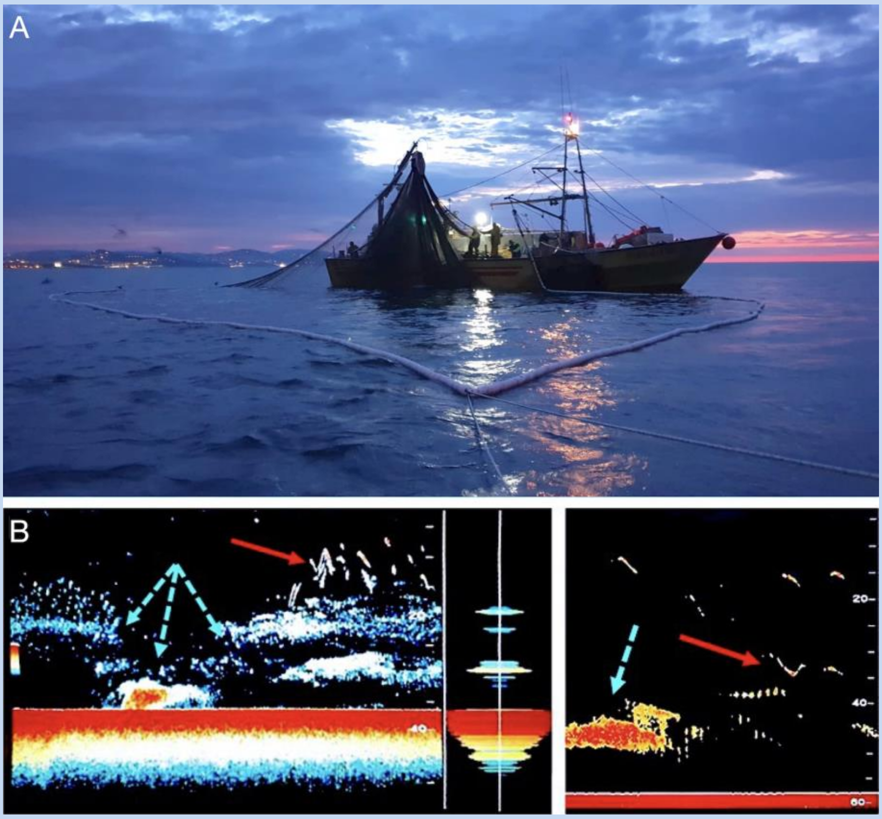

Figure I: Purse seining fishing of small pelagics. Fisheries-induced changes of shoaling behaviour can make fish hard to locate and capture for fishers with socio-economic repercussions on fisheries and local communities. A) a purse seiner fishing boat hauling in the net. B) imaging of an echo sounder on a purse seiner during small pelagic fishing in the North-Western Mediterranean Sea (light-blue dashed arrows indicate shoals of small pelagics, and red solid arrows indicate tunas). Photos copyrighted and courtesy of the Catalan Institute for Ocean Governance Research / Susana L. Díez González and Josep Palaus.